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# Stabilization of organic matter in soils: drivers, mechanisms, and analytical tools - a literature review

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**ABSTRACT:** Soils are the largest terrestrial carbon (C) reservoir, and most of this C is retained as soil organic matter (SOM). Due to its ability to capture, stabilize, and store C for extended periods, soils are considered important allies in decarbonizing the atmosphere. The term ‘C stabilization’ includes a series of mechanisms or processes by which soil C is protected within soils and its losses are reduced through microbial decomposition or leaching. Due to their relevance in the global C cycle, C stabilization mechanisms have received intensive attention from the scientific community. As new analytic technologies push the boundaries of what was previously possible to know, new paradigms emerge. This literature review summarizes the current knowledge of the main mechanisms that may promote SOM stabilization. Factors that govern accumulation of SOM are also addressed. We highlight the role of organo-mineral associations and spatial inaccessibility of SOM due to occlusion within soil aggregates to understand the relative contribution of these mechanisms in different soil conditions (e.g., soil texture, mineralogy, and land-use). In addition, the contribution of cutting-edge approaches and analytical techniques to advance the understanding of SOM protection is presented. Modern techniques to evaluate SOM on a micro, nano, and molecular scale can contribute to the mechanistic understanding of SOM stabilization and the study and adoption of management strategies that maintain and increase C stocks in soils.

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**Received:** October 07, 2022

**Approved:** September 29, 2023

**How to cite:** Carvalho ML, Maciel VF, Bordonal RO, Carvalho JLN, Ferreira TO, Cerri CEP, Cherubin MR. Stabilization of organic matter in soils: drivers, mechanisms, and analytical tools – a literature review. *Rev Bras Cienc Solo*. 2023;47:e0220130. <https://doi.org/10.36783/18069657rbcs20220130>

**Editors:** Cimélio Bayer .

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## INTRODUCTION

Anthropogenic effects on the Earth's climate have become increasingly evident over the last century. Frequency and intensity of extreme temperatures have increased, as well as the variation in rainfall and the rising of ocean levels (IPCC, 2023). In such a scenario, soils play a key role in atmosphere decarbonization, since they represent the largest terrestrial carbon reservoir (1505 Pg) (Lal, 2004). As the main regulator of C exchanges between the atmosphere, terrestrial vegetation, and aquatic environments, soil organic matter (SOM) responds to a dynamic equilibrium maintained between C gains and losses (Lal, 2006). When high C inputs in the form of SOM are associated with reduced losses, soils behave as efficient C sinks, contributing to mitigating global warming and climate change (Eglin et al., 2010; Tang et al., 2019). Furthermore, SOM-rich soils are highly efficient in ensuring the provision of multiple ecosystem services, such as maintaining biodiversity and improving water quality (Hoffland et al., 2020). Therefore, the study, development, and adoption of soil management strategies aiming to promote SOM stabilization and accumulation (e.g., reforestation, erosion control, crop rotation, and minimal soil disturbance) are pivotal to global climate change adaptation and mitigation (Vermeulen et al., 2019; Lal et al., 2021). Advancing the understanding of the SOM stabilization mechanisms and the C dynamics in soils is fundamental for adopting management practices that will enrich the terrestrial C reservoir and improve soil health through increased SOM levels (Dignac et al., 2017).

Soils are an extremely heterogeneous system, formed by a wide range of organic and mineral components, and contain a great variety of living organisms, which coexist in a complex spatial arrangement and pore spaces at different scales. The extreme complexity and heterogeneity of soils create both technical and analytical difficulties that limit researchers' ability to obtain quantitative information at the microscopic and molecular levels on the chemical, physical, and biological processes that govern soil C dynamics (Schmidt et al., 2011; Kravchenko and Guber, 2017). Thus, despite the SOM stabilization mechanisms being widely investigated and described by the scientific community (Six et al., 2002; Kaiser and Guggenberger, 2003; Lützow et al., 2006; Mikutta et al., 2009), few studies describe at a mechanistic level how biotic and abiotic factors may affect C dynamics in soils, especially in soils from the tropics.

Emerging information on the SOM protecting mechanisms against microbial decomposition assumes that its persistence – for decades, centuries, or even millennia – is determined by the soil environment (Schmidt et al., 2011) and not solely by its molecular composition, which would, theoretically, promote selective preservation according to structural and chemical complexity gradients (Kleber, 2010; Dungait et al., 2012). For example, the inaccessibility of SOM due to soil aggregation (Six et al., 2002) or more intimate associations, such as the formation of chemical bonds between organic matter (OM) and soil minerals (Kaiser and Guggenberger, 2003; Kögel-Knabner et al., 2008), are now considered key to SOM protection (Lützow et al., 2006). However, what makes mineral-associated OM inaccessible to the microbiome or the factors that promote the spatial diversity of microorganisms and enzymes remains poorly understood.

Microorganisms role in C dynamics cannot be neglected, since soil microbiome directly influences the decomposition and stabilization of SOM over time (Wieder et al., 2015; Bhattacharyya et al., 2022) and, thus, governs its biogeochemical cycling (Jansson and Hofmockel, 2020). Therefore, a comprehensive understanding of the biotic factors that govern SOM dynamics is critical to better elucidate the mechanisms involved in SOM stabilization (Chenu and Stotzky, 2001). To better understand how SOM is protected against microbial decomposition, SOM is usually separated into conceptual reservoirs according to its decomposition rate (Lützow et al., 2006). However, this classification brings little information on SOM dynamics, its persistence, and the capacity of soils to store C. Other approaches, based on SOM physical fractionation (e.g., particulate organic

matter - POM - and mineral-associated organic matter - MAOM), may help advance knowledge on the stabilization mechanisms (Lavalée et al., 2020). Additionally, detailed information on the chemical and biological processes contributing to SOM accumulation can be obtained through advanced high-resolution techniques, including X-ray Computed Tomography, as described by Lehmann et al. (2008), Vogel et al. (2014), and Kögel-Knabner and Rumpel (2018).

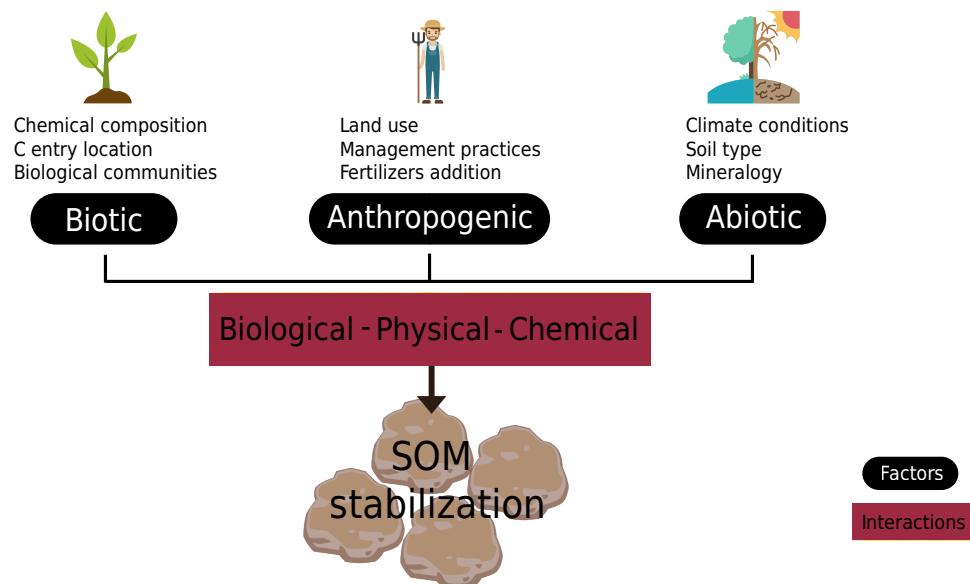
This review aims to synthesize and organize state-of-the-art research focused on the mechanisms that lead to the formation and persistence of SOM and highlight research gaps remaining in SOM stabilization mechanisms in soils within the tropics. Additionally, we compiled how the advanced analytical techniques and approaches have improved the scientific knowledge of SOM dynamics, and how they can create research opportunities for the mechanistic elucidation of the processes that govern the physical and chemical SOM protection.

### **Soil Organic Matter Stabilization Pathways**

Development of strategies to decarbonize the atmosphere based on the potential of soil to sequester atmospheric C requires a better understanding of the interactions between vegetation, soil, and the atmosphere. Litter (i.e., plant-derived organic material provided above the soil) deposition, root decomposition, and plant exudation are the main drivers of C budget in soils (Six et al., 2002; Sokol et al., 2019). Most of the soil C accumulated through plant inputs returns to the atmosphere in the form of CO<sub>2</sub> through soil respiration (Jones et al., 2009; Castellano et al., 2015), and the remaining C may be stabilized to reach longer residence times (Lal, 2004; Lützow et al., 2006; Sokol et al., 2019). The mechanisms thought to determine soil C persistence are intrinsic recalcitrance, spatial inaccessibility (or physical protection), and adsorption to minerals surfaces (Six et al., 2002; Lützow et al., 2006; Schmidt et al., 2011; Dungait et al., 2012). Although treated individually, these act simultaneously in all soils, in response to synergistic and antagonistic effects. For example, biochemical composition governs the sorption kinetics on mineral surfaces, with high-affinity molecules such as aromatic compounds being selectively removed from the soil solution for the formation of mineral-associated organic matter (Chen et al., 2022). The relative importance of each mechanism depends on soil biogeochemical condition, and, ultimately, the soil formation factors. Two are the main pathways that may promote SOM stabilization (i) the biotic pathway: mechanisms related to plants, fauna, and microorganisms, and (ii) the abiotic pathway, which is related to the spatial location of SOM and organo-mineral interactions (Dignac et al., 2017). Additionally, anthropogenic factors such as land-use and management practices may change C dynamics and, thus, must also be considered (Figure 1).

Knowledge of how SOM is stabilized has advanced rapidly in the past decades. The concept of biochemical recalcitrance is no longer considered the main mechanism responsible for SOM persistence, because molecules formerly considered more persistent (i.e., lignins and lipids) may have a rather fast decomposition (Schmidt et al., 2011; Lehmann and Kleber, 2015). In addition, recent studies have detailed the important roles of C allocation from plants, soil biota, aggregates, and structure, which also control SOM dynamics and accumulation (Frouz, 2018; Pausch and Kuzyakov, 2018; Cotrufo et al., 2019; Kravchenko et al., 2019; Button et al., 2022).

The basic principles that affect SOM turnover and stabilization are applied to temperate, subtropical, and tropical climate zones. However, characteristics inherent to the different soils and, thus, the biogeochemical environment, both on the macro and micro scales, define its capacity to retain and protect SOM (Schmidt et al., 2011). Therefore, most current models that attempt to predict SOM dynamics consider several factors that control SOM turnover, including site-specific factors such as mineralogy (Torn et al., 1997; Kaiser and Guggenberger, 2003; Kramer et al., 2012) or the quantity and chemical quality of the litter (Sayer, 2006; Huang and Spohn, 2015). However, the mechanistic processes by which local properties contribute to C stabilization are still poorly understood.



**Figure 1.** Determining drivers, factors, and interactions in the SOM stabilization processes.

### SOM Inputs and the Concept of Biochemical Recalcitrance

#### ***SOM inputs: litter and rhizodeposition***

Plants add C to the soil mainly through: (i) litter produced from roots and shoots and (ii) root exudates and other organic substances released in plant rhizospheres (Kuzyakov and Domanski, 2000; Pausch and Kuzyakov, 2018).

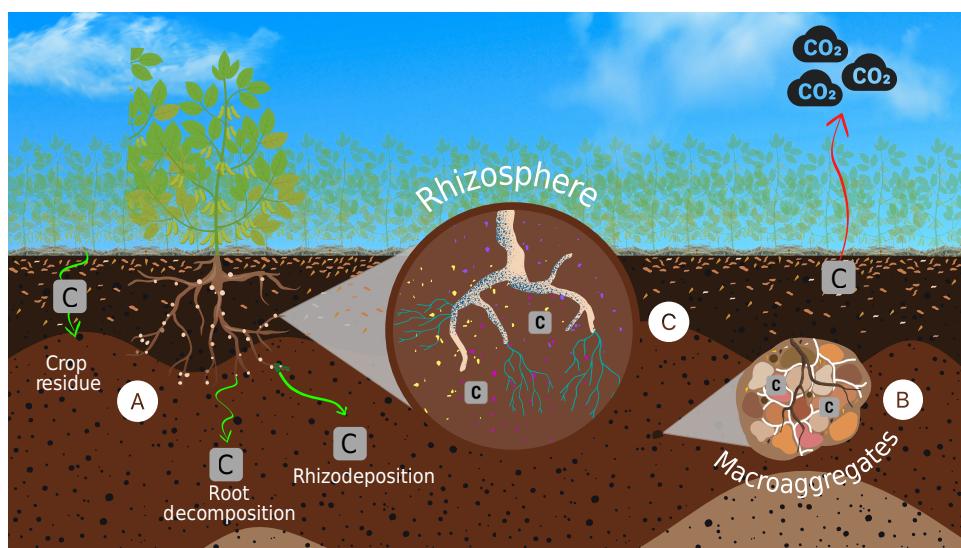
Most organic matter supplied aboveground is retained in the upper soil layers (mainly as POM) and quickly decomposed or translocated to deeper layers (Liebmann et al., 2020). In the past, it was assumed that the quantity and quality of structural residues deposited aboveground were responsible for maintaining and/or increasing C levels in soils. However, scientific advances have shown that approximately 40 % of the C fixed by plants is allocated belowground through plant roots (Jones et al., 2009), which surpass the aboveground inputs for the formation of stable SOM (Balesdent and Balabane, 1996; Rasse et al., 2005; Kätterer et al., 2011).

Carbon from dead roots has a soil residence time of ~2.4 times longer than from litter (Rasse et al., 2005). The greatest contribution of roots to stabilized SOM may be attributed to their chemical composition (Jobbágy and Jackson, 2000) and their wide distribution and intimate interaction with minerals, microorganisms, and aggregates in soils (Rumpel et al., 2015; Baumert et al., 2018). Roots tend to have more aliphatic compounds which are quickly adsorbed to mineral surfaces (Jobbágy and Jackson, 2000). Such composition allows a greater efficiency in the use of carbon by microorganisms, which promotes microbial growth, while its products favor stable SOM formation (Cotrufo et al., 2013). Additionally, the distribution of root systems in the soil profile strongly influences the dynamics of SOM at depth (Ota et al., 2013), mainly because the supply of fresh OM is limited in deeper layers (Chabbi et al., 2009), as confirmed by isotopic studies (see Mendez-Millan et al., 2010).

Most plant species modify their rhizosphere's microbiome to enhance nutrient acquisition (Jansson and Hofmockel, 2020). Some symbiotic microorganisms, commonly recruited by plants (e.g., nitrogen-fixing bacteria and mycorrhizal fungi), may influence the soil aggregate formation and contribute to residues that 'feed' the SOM reservoir. The release of organic compounds by plant roots (i.e., rhizodeposition) is an important source of organic C and is responsible for several physical, biological, and chemical processes in the soil (Jones et al., 2009). Rhizodeposition has been reported to regulate water

flow (Moradi et al., 2012), C turnover and sequestration (Kögel-Knabner, 2007), and the activity of microbial communities (Nguyen, 2009). Root association with arbuscular mycorrhizal fungi increases net rhizodeposition and, thus, the accumulation of SOM in the rhizosphere (Zhou et al., 2020).

Different root compounds can be released as rhizodeposits, including carbohydrates, amino acids, fatty acids, and phytohormones (Jones et al., 2009), which are ultimately metabolized by microorganisms (Hees et al., 2005; Jones et al., 2009). Renewal of root border cells, the senescence of epidermis and root hairs, mucilage secretion, and volatilization can source these compounds into the rhizosphere (Jones et al., 2009). Unlike the C derived from shoots, which are composed of structural polymers, rhizodeposits are mainly composed of low-molecular-weight organic compounds. Soil microorganisms easily metabolize these compounds and have high MAOM formation efficiency (Hees et al., 2005; Jones et al., 2009; Villarino et al., 2021), however, when added in large amounts, often change the rate of native SOM mineralization (Huo et al., 2017), through a process widely known as the *priming effect* (Kuzyakov, 2010). Dissolved low-molecular weight C compounds present in the dissolved organic matter (DOM) fraction are an efficient precursor to SOM formation. Water-soluble fraction of DOM is the primary agent in MAOM formation, either through direct adsorption to mineral surfaces or assimilation by microorganisms and conversion to microbial-derived compounds, which in turn associate with the mineral fraction (Cotrufo and Lavallee, 2022). While litter-derived DOM influences the formation of SOM closer to the soil surface, DOM derived from root decomposition and rhizodeposition tends to influence SOM formation in deeper soil layers (Yang et al., 2023). However, little is known about these mechanisms in soils from tropical regions (Gmach et al., 2020).



**Figure 2.** Schematic illustration of the plant-microbiome-soil interactions in the rhizosphere and their effects on C dynamics in the soil. (A) Organic C inputs into the soil via root exudates and necromass (inputs represented by the green arrows); (B) Fungal hyphae development (represented in white), associated with the physical action of the roots and mucilage secretion, form macroaggregates which physically protect C. (C) Low molecular-weight-organic compounds released into the rhizosphere are easily metabolized by microorganisms, which synthesize secondary products preferentially associated with the mineral matrix of the soil. Red arrow indicates C losses through respiration.

### **SOM recalcitrance and quality**

Chemical composition of litter and root exudates varies considerably. Plant residues are a complex mixture of polysaccharides, lignin, proteins, waxes, and other components (Lützow et al., 2006). Distribution of such components varies according to the plant species and tissues. Until recently, the chemical and physical characteristics of the added organic material were believed to determine its residence time within the soil, i.e., the rate of decomposition. This view assumed that the organic inputs included both labile (i.e., easily decomposable; such as carbohydrates) and recalcitrant fractions (i.e., complex polymers hard to decompose, such as lignin). The latter would be preserved and decomposed after the labile fraction had been exhausted, thus producing older and more resistant SOM (Marschner et al., 2008; Kleber, 2010). Plant tissues with the highest C:N ratios and lignin contents were considered more resistant to decomposition – a compound with a polymeric and disordered aromatic structure, which can be more efficiently co-metabolically degraded (Kuang et al., 2018). Since lignin represents approximately 20 % of the plant litter (Gleixner et al., 2001), it has been considered a major SOM component, directly influencing the soil C reservoirs and persistence (Thevenot et al., 2010). However, contrary to previous assumptions, a new paradigm shows that microorganisms could consume such “persistent” materials under the right soil conditions before assessing the more labile forms (Lehmann and Kleber, 2015). Currently, the amount of stable SOM is considered a result of the joint action of biotic and abiotic factors (Schmidt et al., 2011), while biochemical recalcitrance plays a secondary role in the persistence of SOM (Marschner et al., 2008).

Chemical composition of organic molecules would play a major role in the initial stages of decomposition, which cannot be extrapolated to time-spans of decades to millennia (Dungait et al., 2012). Metabolization of complex molecules such as lignin may be advantageous, since smaller and more soluble molecules may provide little energy (Lehmann et al., 2020). Thus, some chemically simple molecules would persist in the soil for longer periods. Fox et al. (2006) demonstrated that soil fauna can specifically use organic compounds that contradict the classical recalcitrance sequence. Additionally, analysis of the residence time of different biomolecules showed that no single compound appears to be more recalcitrant (Schmidt et al., 2011). Recalcitrance as the dominant mechanism of SOM stabilization may be considered in specific soil environments, as in the case of the “Terra Preta de Índio”, anthropogenic soils with high OM contents, resulting from the accumulation of plant and animal residues, large amounts of ash and partially carbonized residues (i.e., charcoal), which evidence soil use and occupation by indigenous populations (Novotny et al., 2007; Glaser and Birk, 2012). Still, the aromatic nature of charcoal alone would not guarantee the persistence of C for long periods. Therefore, factors such as hydrophobicity, organo-mineral interactions, and microbial community composition also play a role in limiting microbial decomposition in these cases (Bento et al., 2020; Liu et al., 2022).

### **Mechanisms of SOM Protection**

#### **Organomineral interactions**

Persistence of SOM, especially on a millennium scale, has been attributed to the sorption of organic compounds to reactive sites on the surface of minerals (Cotrufo et al., 2015; Kleber et al., 2015). Such associations are considered to stabilize and protect SOM against microbial decomposition (Kaiser and Guggenberger, 2003; Kögel-Knabner et al., 2008; Kleber et al., 2015), and, in certain environments, such as acid soils with mineralogy predominantly composed of poorly crystalline minerals, may represent more than 90 % of SOM reflecting in turnover times four-fold longer than free or occluded OM (Kleber et al., 2005). This supports the hypothesis that organic compounds with different degradation rates may be stabilized and persist in the environment through the formation of organo-mineral associations (Dungait et al., 2012; Hemingway et al., 2019). Soil mineral

composition is important for SOM protection, as minerals within the clay-size fraction (i.e., <2 µm) have reactive surfaces that can interact with organic molecules (Chenu and Stotzky, 2001). Soil minerals with particle sizes <53 µm are reported to participate in the formation of organo-mineral associations (Kleber et al., 2015). Clay minerals and iron oxyhydroxides have been shown to efficiently protect SOM from decomposition (Sollins et al., 2009) through different mechanisms, such as ligand exchange, polyvalent cation bridging, hydrogen bonds, and van der Waals forces (Lützow et al., 2006). Evidence suggests that chemically stabilized OM has a reduced mineralization rate (Eusterhues et al., 2003) since microorganisms and enzymes are not able to break the existing chemical bonds between OM and soil minerals (Chenu and Stotzky, 2001).

### ***Clay minerals and iron oxyhydroxides in highly-weathered soils***

Several studies consider soil mineralogy and initial SOM contents as the two key factors that determine whether plant residues will be protected within aggregates or stabilized as MAOM (Six et al., 2002; Kaiser and Guggenberger, 2003; Stewart et al., 2008; Poirier et al., 2013). Although soils with high clay contents tend to have a greater capacity to retain C (Six et al., 2002; Carter et al., 2003), clay mineralogy may influence soil properties (e.g., specific surface area - SSA, cation exchange capacity - CEC, and charge density), affect the sorption capacity and soil aggregation, and, ultimately, SOM mineralization rates (Baldock and Skjemstad, 2000; Kögel-Knabner et al., 2008). Soil organic matter is stabilized mostly through sorption by clays (Kleber et al., 2015); and, therefore, clay activity may affect SOM retention. However, different studies suggest that high-activity clay soils do not always retain more SOM than those dominated by low-activity clays (Feller and Beare, 1997; Hassink, 1997; Wattel-Koekkoek et al., 2001). The potential of highly weathered soils to retain SOM could partially be explained by the dominance of Fe and Al oxides in the clay fraction (Kaiser and Guggenberger, 2003; Tombácz et al., 2004; Rasmussen et al., 2018). Due to their high reactivity, large surface area, and sorption sites, Fe and Al oxides play an important role in the formation of organo-mineral associations both in soil surface (Rasmussen et al., 2006) and subsurface layers (Kleber et al., 2005).

Iron oxyhydroxides, especially in poorly crystalline forms, are reported to have high SSA (Specific Surface Area) and densities of reactive hydroxyl sites, which favors the interaction with SOM. Organic compounds were reported to be preferentially protected by the interaction with poorly crystalline minerals (Kleber et al., 2015; Porras et al., 2017). Evidence suggests that the formation of Fe-OM complexes is the main determining factor for rhizocarbon stabilization in highly weathered soils (Jeewani et al., 2020). Iron oxyhydroxides are also strongly related to soil aggregation and, thus, contribute to the stability of aggregates (Six et al., 2002). The formation of stable aggregates provides excellent protection for C within macro- and microaggregates, allowing sufficient time to strengthen the bonds between OM and the reactive sites on mineral surfaces (Briedis et al., 2018).

Although the relative importance of Fe and Al (hydro)oxides in SOM stabilization has been recognized for some time, these minerals have a wide spectrum of crystallinities and reactivities in soil and are influenced by different environmental conditions (e.g., soil pH and Eh). Recent studies suggest that the reductive dissolution and reprecipitation of Fe oxides, under redox cycles, can lead to an increase in poorly crystalline Fe phases (Winkler et al., 2018; Queiroz et al., 2022). Therefore, the wetting and drying cycles, among other factors, may control the transformation of Fe oxides in soils and favor the formation of organo-mineral associations or, in anoxic events, favor the release of the SOM as soluble or colloidal forms (Hall et al., 2018). However, the distribution of SOM associated with Fe and Al (hydro)oxides of different crystallinities has not been well quantified, limiting the knowledge of their role in the stabilization mechanisms operating between SOM and these minerals (Heckman et al., 2018).

### **Carbon saturation**

In contrast to traditional models of SOM dynamics, which assumed an indefinite and linear increase in SOM with increasing C input (Stewart et al., 2007), evidence has shown a limit to C accumulation suggesting the concept of C saturation (Six et al., 2002; Stewart et al., 2007). Although little is known about C saturation in highly weathered soils, Santos et al. (2011) found an asymptotic relationship between root C inputs and mineral-associated C in a subtropical Ferralsol, indicating that C saturation may occur in such soils. Similarly, Briedis et al. (2016) found that mineral-associated C tended to saturate Brazilian soils under subtropical climates. This potential is even greater in the subsurface layers, where C contents are lower (Briedis et al., 2018). According to Feng et al. (2014), C saturation is more likely to be reached by MAOM, reflecting the finite SSA in minerals for the establishment of organo-mineral interactions (Hassink, 1997). Nevertheless, the accumulation of SOM in the form of POM is not subject to saturation (Lavallee et al., 2020a). Rodrigues et al. (2022) reported that soils in long-term no-till systems continue C accrual, even as the C saturation threshold approaches, by preferential accumulation in the POM fraction. This allows the accumulation of SOM in compartments with high storage and protection potential, through the adoption of management practices, such as minimal soil disturbance and high biomass input, which can be used as an effective strategy to increase C sequestration (Cotrufo et al., 2019).

### **Physical protection of SOM**

For microbial OM decomposition, microorganisms and/or their enzymes must be in direct contact with the OM under local conditions that favor microbial activity. Due to soil spatial heterogeneity (i.e., the spatial arrangement between its constituents), the compartmentalization of enzymes, substrates, water, oxygen, and microorganisms has a significant impact on SOM dynamics (Totsche et al., 2018). The entry route of C, as well as its subsequent location in the soil, defines its accessibility to biological communities. Based on these concepts, stable macro- and microaggregate formation may physically protect SOM through occlusion (Six et al., 2002; Lützow et al., 2006; Huang et al., 2010), which: (i) reduces the contact of microorganisms and enzymes with OM, (ii) restricts aerobic decomposition due to the reduced oxygen diffusion, especially within microaggregates, and (iii) compartmentalizes the diffusion of enzymes in intra-aggregate pores (Six et al., 2002; Lützow et al., 2006).

Evidence of OM occlusion within soil aggregates is widely reported in the literature both for soils under temperate (Lützow et al., 2006) and tropical climate conditions (Amado et al., 2006; Dieckow et al., 2009; Briedis et al., 2018; Franco et al., 2020). The aggregation hierarchy as proposed by Tisdall and Oades (1982) can be triggered by the physical attachment of roots and hyphae in macroaggregates (Jiménez and Lal, 2006). After roots and hyphae die, the macroaggregate's stability is reduced, increasing their susceptibility to breakage and exposure to the protected OM. For highly weathered oxidic soils, where Fe and Al oxides and hydroxides are the dominant stabilizing agents, the concept of aggregation hierarchy should be applied with caution (Oades and Waters, 1991). Adoption of conservationist management strategies may favor soil aggregation, and, thus, are essential to increase C sequestration in highly weathered soils (Wiesmeier et al., 2012). Management practices, including no-till, are known to promote C accumulation in surface soil layers (Zinn et al., 2005; Nicoloso et al., 2018) since preserved aggregates can retain approximately 90 % of the OM through occlusion (Rabot et al., 2018). However, studies show that the benefits of no-till on C stocks can also occur in deeper soil layers (up to 1.0 m) (Boddey et al., 2010; Gauder et al., 2016; Briedis et al., 2018). Thus, to achieve a more comprehensive understanding of the effect of management practices and land-use change on C stocks and SOM stabilization, soil sampling cannot be limited to surface layers, as more than 50 % of the SOM is stored below the first 0.30 m (Batjes, 2014).

### **Contributions of soil porosity to SOM physical protection**

Mechanisms that prevent or limit SOM decomposition by microorganisms are controlled by the distribution and size of pores (Lützow et al., 2006; Kravchenko and Guber, 2017). The microscale porous architecture regulates several physical, chemical, and biological processes and, thus, directly controls the stabilization of SOM, especially when organic compounds are within pores that are less accessible to microorganisms (Kravchenko et al., 2019; Schlüter et al., 2020). The aggregate's interior may have different properties from the bulk soil, with marked variations in O<sub>2</sub> concentration and water content, providing a heterogeneous niche for microorganisms to occupy (Wilpiszeski et al., 2019). Microorganisms, in turn, can form microbial communities inside or outside the aggregates, according to the existent abiotic factors, resulting in distinct metabolic activities (Ebrahimi and Or, 2016). In fact, some microorganisms may be trapped inside soil aggregates during its formation (Rillig et al., 2017).

Small soil microaggregates are rich in pores <0.2 µm in diameter, which limits its access by bacteria (Lützow et al., 2006). Depending on soil texture, up to 95 % of the soil pore space can be small enough to prevent the movement of bacteria and its access to OM (Veen and Kuikman, 1990). This physical barrier tends to be more relevant for bacteria, as fungi can overcome this impediment by producing hyphae (Ritz and Young, 2004). Since small pores can reduce the accessibility of predators (Vos et al., 2013), pores with diameters between 30 and 150 µm tend to host an extremely high diversity of microbial communities. Therefore, C allocated in such pores is subject to greater losses (Kravchenko et al., 2019). Kravchenko et al. (2015) observed that POM connected to the atmosphere by pores >13 µm suffered losses of up to 15 % of its volume due to the increased oxygen supply promoted by larger and more connected pores, which, in turn, led to greater decomposition of OM. In contrast, OM mineralization rates are reduced by approximately 90 % in anaerobic microsites within soils with high pore discontinuity and tortuosity (Keiluweit et al., 2017, 2018; Li et al., 2017). In addition, solute diffusion is facilitated under high soil moisture contents, while drought events can effectively isolate microorganisms in pores with minimal dissolved nutrients (Schimel, 2018). The balance between O<sub>2</sub> diffusion and resource supply also affects SOM mineralization (Schimel, 2018) so the physical distance between decomposers and the OM within the heterogeneous soil microscale will control SOM dynamics.

### **Soil Organisms and Their Role in Carbon Stability**

#### ***Soil macro- and mesofauna***

Effects of soil macro- and mesofauna on SOM decomposition and stabilization are poorly understood despite their potential effects on SOM dynamics at many spatial-temporal scales (Wiesmeier et al., 2019). Soil fauna may be divided into two main groups according to their body size. Macrofauna is composed of organisms larger than 2.0 mm, mostly including earthworms, termites, ants, beetles, and millipedes (Wallwork, 1970; Briones, 2014). Due to their larger body size macrofauna are known as ecosystem engineers, i.e., they can displace large volumes of soil during their movement, altering soil structure and porosity (Lee and Foster, 1991; Jones et al., 1994; Lavelle et al., 1997), and, ultimately, soil functioning. When soil macrofauna has access to litter, much of it is not mineralized, but rather translocated belowground and incorporated within the mineral layers, mainly as POM (Frouz, 2018). Only a small part of the litter consumed by macrofauna is assimilated; the remainder returns to the soil in the form of feces (David, 2014). As it passes through the intestinal tract of organisms, the litter continues to break up, acquiring a greater surface area. Various microorganisms within the gastrointestinal tract of these organisms increase the microbial decomposition of the ingested material (Kaneda et al., 2013). After a few hours or days, the microbial activity in the stool is reduced and the rate of decomposition slows down. With the aging of the feces, the OM becomes protected and

occluded in the biostructures with small pores and anaerobic conditions, which further delay decomposition (Frouz, 2018).

Soil mesofauna includes organisms with body sizes between 0.2 and 2.0 mm (e.g., mites and springtails). Soil mesofauna exerts an enormous influence on chemical and biological properties, performing detritivorous and predatory functions that impact SOM decomposition and microorganism populations (Siepel and Maaskamp, 1994). Soil mesofauna also breaks down plant residues, facilitating their decomposition by fungi and bacteria. Manipulation experiments showed a significant reduction in litter mass when soil fauna organisms were present, as a result of the direct consumption of plant material and the increase in soil microbial activity (Wall et al., 2008). According to García-Palacios et al. (2013), in the absence of fauna, the litter decomposition rates would be reduced by 35 % on a global scale, with the reduction ranging from 22 to 32 % in tropical regions. Thus, soil macro- and meso-fauna are involved directly and indirectly in SOM decomposition (Filser et al., 2016), and, therefore, future prediction models on SOM stocks should consider their role (Dignac et al., 2017).

### ***Bioturbation and SOM***

Soil macrofauna can influence the distribution of SOM through bioturbation; i.e., the biological reworking of soils (Lavelle, 1988; Meysman et al., 2006). However, the effects of bioturbation in SOM dynamics depend on the ecological groups. Epigeic species inhabit the surface, which is the richest in fresh OM, and contribute little to the redistribution of plant material. In contrast, endogeic species are typically found in deeper soil layers and create underground galleries, actively transporting SOM. Some intermediate species that feed at the surface inhabit deeper layers and are also responsible for transporting large amounts of OM (Lavelle, 1988). Bioturbation is the main process responsible for the vertical distribution of SOM, surpassing roots and leaching. (Tonneijck and Jongmans, 2008). Similarly, Elzein and Balesdent (1995) demonstrated that in many soil types (macro) fauna plays a dominant role in SOM transport. This vital role is diminished in agricultural soils, especially unhealthy soils, in which soil fauna abundance can be considerably lower than in natural ecosystems (Lal, 1988; Velasquez and Lavelle, 2019).

Creation of biogenic structures by these ecosystem engineers may promote SOM stabilization (Lavelle et al., 2020b). These biogenic structures (i.e., excrements and galleries) can stabilize C by promoting organo-mineral associations (Dignac et al., 2017), as organic and mineral particles are mixed and complexed with mucus during the digestive process (Six et al., 2004) and extracellular enzymes are stabilized by sorption onto the surface of minerals (Dove et al., 2020), or by carrying C to deeper soil layers (Don et al., 2008; Button et al., 2022). The shape and stability of the biogenic structures will affect SOM turnover time, which can ultimately be impacted by land-use (Don et al., 2008; Vidal et al., 2016). Franco et al. (2020) found that land-use change has caused significant decreases in SOM stocks coupled with a reduction in the abundance of soil engineers. Additionally, the suppression of ants, earthworms, and especially termites reduced both the formation and the stability of soil aggregates. This process of soil structural deterioration lowers the physical protection of C within the soil aggregates, which indirectly impacts SOM stocks.

### ***Influence of microbial biodiversity on C sequestration***

Soil microbiome consists of bacteria, archaea, fungi, viruses, and protozoa. Among these microorganisms, fungi, and bacteria are the main groups that govern the accumulation and decomposition of SOM. Fungi and bacteria activity produces biopolymers that favor the formation of the aggregates, which can occlude SOM and protect against further microbial decomposition. Chemical composition of persistent SOM is similar to microbial cells and their by-products rather than to plant tissues (Kögel-Knabner, 2017). Therefore, SOM is now understood as a continuum of organic biopolymers continuously processed by soil

microorganisms, which perform various ecological functions. As microorganisms control the dynamics of SOM, the trophic and ecological relationships between microorganisms are directly intertwined with SOM turnover (Lehmann and Kleber, 2015). Additionally, greater C inputs stimulate the activity of symbiotic or free-living microorganisms, increasing microbial biomass and contributing to the C distribution within the soil matrix. These microorganisms are also responsible for the biochemical transformation of C into forms, such as aromatic and aliphatic acids and some nitrogen-rich biomolecules, that are selectively adsorbed to mineral surfaces and, thus, less bioavailable and more persistent over time (Kopittke et al., 2018; Angst et al., 2021).

Mechanistic understanding of how microorganisms regulate soil C processes is a great research challenge due to the complexity and dynamic of microbial communities. Thus, bioindicators may minimize microbial complexity's effects and produce elegant information on microbial processes. Fungus:bacteria (F:B) ratio is an indicator widely incorporated in some ecological models to understand the impact of environmental changes on soil C sequestration (Strickland and Rousk, 2010). Different F:B ratios are directly associated with variations in C stocks. (Malik et al., 2016). For example, the dominance of fungal communities tends to favor SOM accumulation and reduce its turnover time, increasing the capacity of soil to sequester C. Fungi are the main decomposers of SOM, as they are highly versatile and more persistent than any other microorganism. Compared to bacteria, fungi have lower energy demand and, thus, can more efficiently transform organic substrates into microbial components (Cotrufo et al., 2013). Up to 50 % of the decomposed substances can be transformed into fungal tissues. In addition, more than 90 % of higher plants have symbiotic associations with mycorrhizal fungi, which favors the absorption of nutrients by the roots, besides improving the soil microenvironment (Smith et al., 2011).

Mycorrhizal fungi inhabit a small interface between plant roots and the soil, and several fungal mechanisms can potentially influence the stabilization of SOM. Mycorrhizal fungi carry part of the photoassimilates from plants to their rhizospheres, and distribute plant-derived C to the entire soil matrix, favoring organo-mineral interactions and stimulating the activity of free-living decomposers. Tissue death or renewal also contributes to microbial necromass, which is another important source for the formation of stable SOM (Cotrufo et al., 2013). Furthermore, mycorrhizal fungi help to form and stabilize aggregates, favoring SOM physical protection (Six and Paustian, 2014). This suggests that increasing the fungal symbiosis with plants can improve C sequestration (Trivedi et al., 2013; Hannula and Morriën, 2022).

### ***Manipulation of soil microbial communities***

Manipulation of soil microbiome can be done through the introduction of microorganisms or by changes in the vegetation cover (Jastrow et al., 2007). According to Demenois et al. (2017), inoculation of selected mycorrhizal fungi into soils in tropical regions improved the accumulation and protection of SOM. No-tillage and the use of cover crops also favor the growth of fungi and contribute to the stabilization of soil aggregates (Helgason et al., 2010; Veloso et al., 2019). Management strategies to increase C sequestration must consider competitive and enabling interactions between microbial communities, and the spatial-temporal dynamics of microorganisms within the soil throughout their life cycle (Kallenbach et al., 2019). This may ensure its potential to catalyze reactions that produce more recalcitrant and stable microbial products.

The era of “omics” and molecular tools enables the characterization of biological communities and assessment of the role of different microorganisms in SOM transformations (Dignac et al., 2017). Studies using data from multi-omics (metagenomics, metatranscriptomics, and metaproteomics) can provide detailed information on the taxonomy, phenotypic characteristics, and metabolic functions of soil microbial communities. In tropical regions, wetting and drying cycles will become more frequent in response to climate change

(O'Connell et al., 2018), which may accelerate SOM losses. Multi-omic tools can help clarify how such cycles will affect the structure and function of soil microbiomes, including changes in the expression of specific metabolic pathways and the selection of adaptive species, which will ultimately impact the soil C cycle (Chowdhury et al., 2019).

Long-term experiments can also help elucidate how microbial communities modulate C dynamics in soils. To overcome soil complexity, studies have used simplified microbial communities in controlled environments aiming to simulate soil on micro- and meso scales (Goldford et al., 2018; Zegeye et al., 2019). Using a reduced number of microbial communities allows a more accurate determination of the key mechanisms that govern microbial ecology and their relationship with C sequestration. Advancing knowledge on microbial ecology provides an understanding of how microorganisms use C and, therefore, affect its long-term fate within the soil (Schimel and Schaeffer, 2012). Assessing and tracking stable isotopes represents a powerful approach to determining the fate of organic C in the soil (Naylor et al., 2020). The  $^{13}\text{C}$  isotopic tracers determined the contribution of microbial biomass to stable SOM formation (Schweigert et al., 2015), as well as the relative contribution of bacterial vs. fungal necromass in tropical forests (Throckmorton et al., 2012). Such information improves the understanding of how different microbial groups contribute to the maintenance and accumulation of SOM.

## SOM Evaluation Approaches and Analytical Techniques

### *Initial stages*

Knowledge of SOM dynamics and formation has undergone great transformation over the last few decades due to the evolution of analytical techniques. Until the mid-1990s, when the biochemical recalcitrance of organic molecules was considered the main mechanism for SOM stabilization, laboratory techniques to extract and purify humic substances (i.e., humic acid, fulvic acid, and humins) were the most applied (Lehmann and Kleber, 2015). These techniques, which define SOM in terms of solubility and chemical recalcitrance, provided little information to describe and predict the dynamics of SOM. Contrastingly, in the current paradigm, studies based on the chemical extraction of SOM are widely criticized, as there is no evidence that the chemically extracted material naturally exists in soils and, therefore, should not be used to characterize the composition and turnover of SOM (Lehmann and Kleber, 2015).

To understand the stability of SOM and its turnover, researchers began to integrate incubation studies (Pronk et al., 2013), radiocarbon dating, and separation of soil aggregates (Trumbore, 2009), as well as other methods to compartmentalize SOM in different reservoirs, with different characteristics and turnover times. Assessing and tracking stable isotopes still represents a powerful approach to determining the fate of organic C in the soil (Naylor et al., 2020). The  $^{13}\text{C}$  isotopic tracers determined the contribution of microbial biomass to stable SOM formation (Schweigert et al., 2015), as well as the relative contribution of bacterial vs. fungal necromass in tropical forests (Throckmorton et al., 2012), information that improves the understanding of how different microbial groups contribute to the maintenance and accumulation of SOM.

### *Physical fractionation methods*

As the paradigm of SOM stabilization developed, SOM physical fractionation methods based on size and/or density became preferable over chemical extraction methods. Several SOM fractions with contrasting behaviors started to be obtained. The POM and MAOM are easy to obtain and considered key promising fractions, for scientists to understand and predict the SOM dynamics on different scales (Lavallee et al., 2020a). Regardless of the fractionation method used, evaluating the mechanisms that ensure SOM stabilization

is not a simple task. For that, measurements and observations must be conducted to support, for example, the physical protection of the SOM or the organo-mineral interactions. Advances in analytical techniques have expanded the knowledge of SOM stabilization mechanisms, the ability to characterize SOM, and information on the factors that regulate its fate. Each approach to SOM assessment allows for the understanding of a process or mechanism responsible for its formation, its role in the environment, and its turnover. The best strategy or analytical technique to characterize SOM depends on the research objectives (Table 1) and the available methods and multidisciplinary approaches that have not been well integrated yet. Future advances will be achieved by integrating the evaluation of (*i*) the chemistry of SOM, (*ii*) biological communities and their action on SOM, and (*iii*) soil structure at small spatial scales.

**Table 1.** Synthesis of the methods used in the studies about SOM stabilization mechanisms and the type of information obtained from each evaluation approach

Category of the method	Examples of methods	Information obtained
Fractionation methods	Densimetric or granulometric fractionation	SOM location; physical and chemical properties; quantification of SOM in different fractions (POM and MAOM)
	Solubility in acids and bases	Physical and chemical properties of humic substances
Characterization methods	Elementary analyzes	The elementary composition of SOM
	Infrared spectrometry	Functional groups; ability of SOM to interact with metals; condensation index
	Nuclear magnetic resonance (NMR)	Identification and quantification of functional groups; Structural composition
	<i>Near Edge X-ray Absorption Fine Structure</i> (NEXAFS)	Chemical composition of SOM; functional groups; C content and origin
Isotopic methods or incubation assays	Tracing natural $^{13}\text{C}$	Origin of SOM (C3 or C4)
	$^{14}\text{C}$ Dating	SOM residence time
Visualization methods	Scanning electron microscopy	Identification and distribution of organic components on the soil surface
	X-ray computed tomography	SOM location; porous architecture, distribution of biological, organic, and mineral constituents
	NanoSIMS	Isotopic and elementary map of OM on the surface of mineral particles
	<i>Scanning Transmission X-ray Microscopy</i> (STXM)	Structural characterization of soil microaggregates that provide SOM stabilization
	<i>Near Edge X-ray Absorption Fine Structure</i> (NEXAFS)	Distribution of C forms on the mineral surface

### SOM chemical composition analysis

A major obstacle to understanding SOM dynamics is its complex and heterogeneous composition, resulting from the mixture of plant constituents, transformed organic compounds, microbial cells, and products of microbial metabolism (Kögel-Knabner, 2007; Sierra et al., 2011). Several processes occur on a molecular scale, so the characterization of the molecular composition of SOM is essential to understanding the origin and formation, and the processes that control its dynamics. The use of gas chromatography to investigate the structural composition of humic and fulvic acids allowed the first major steps in the characterization of SOM (Stevenson et al., 1970; Stevenson, 1982). Additionally, the use of pyrolysis to break the humic fractions into identifiable units for further separation by gas chromatography (Schnitzer and Khan, 1978) also allowed significant advances. With this approach, strong evidence emerged supporting the hypothesis that aromatic structures linked to aliphatic chains formed the basic unit of humic substances, which placed lignin as the main plant constituent precursor of SOM. During the 1980s, pyrolysis coupled with gas chromatography and mass spectrometry (Pi-CG/MS) gained prominence in the recognition of individual characteristics of the SOM structures (Saiz-Jimenez, 1992). With a more detailed qualitative analysis provided by Pi-CG/EM, new products found in humic fractions could be characterized, contributing to the understanding of the chemical nature of plant components present in humic acids and providing new insights into the central role of lignin as the precursor for the formation of humified SOM (Saiz-Jimenez and De Leeuw, 1986; Schulten and Schnitzer, 1992).

During the same period, the use of infrared (IR) spectroscopy increased, mainly because it is a non-invasive method that can analyze humic isolates (Kögel-Knabner and Rumpel, 2018). Relevant information about the functional groups of fulvic and humic acids was obtained, detailing the structural arrangement or the type of bonds present (Bailly, 1974). The E4/E6 ratio, defined as the ratio between absorption at 465 and 665 nm, was also widely used to infer the structural properties of humic substances, such as the proportion of aliphatic or aromatic components (Chen et al., 1977). However, recent studies with greater experimental rigor evidenced that the E4/E6 ratio provides little information on the concentration of aromatic rings.

In the search for better structural information on the SOM, scientists also began to analyze the chemical composition of the physical fractions obtained by the densimetric or granulometric fractionation methods. One of the first techniques used in this period was Pi-CG/MS coupled with solid-state nuclear magnetic resonance (NMR), intending to observe the general structure of SOM through the detection of its functional groups (Kögel-Knabner et al., 1992). Applying such solid-state techniques, Kögel-Knabner (1993) found that aromatic forms of C did not dominate the SOM composition in many soils, indicating that aromatic compounds did not accumulate in the soil during SOM formation, whereas the clay fraction showed an increased content of aliphatic C (Baldock et al., 1992, 1997). The increase in the aromatic carbon content in the larger size fractions supported the selective preservation mechanism. However, the interaction of organic compounds with the clay fraction was still poorly understood and the chemical composition of SOM within the soil profile started to be associated with soil classes and pedogenic processes (Quideau et al., 2001). Through these findings, many studies began to combine the physical fractionation and chemical characterization of SOM (Kögel-Knabner, 2000; Lützow et al., 2007; Cao et al., 2011), enabling the identification of the factors and mechanisms involved in the formation and persistence of SOM and creating a broader view on the structure and functioning of SOM (Lützow et al., 2007). Molecular analyses of physical SOM fractions revealed that microbial products can be preferentially stabilized by interactions with soil minerals (Larré-Larrouy et al., 2003), mainly Fe and Al oxides (Lützow et al., 2006) and that the composition of SOM can be influenced by soil type (Spielvogel et al., 2008), depth (Rumpel and Kögel-Knabner, 2011), and land use (Helfrich et al., 2006; Cusack et al., 2013).

### ***Three-dimensional analytical techniques***

Chemical composition of SOM, along with its physical and chemical properties define its reactivity, which, in turn, regulates its interaction with the mineral matrix (i.e., organo-mineral interactions or protection within soil aggregates). Therefore, SOM stabilization came to be understood as dependent on the three-dimensional arrangement of soil minerals, organic matter, microbiome, and other components, such as air and water. Detailed studies using high-resolution techniques could overcome the spatial complexity of soil as well as the chemical complexity of SOM, providing new insights into its stabilization and accumulation.

Nanoscale secondary ion mass spectroscopy (NanoSIMS) is an improvement of the SIMS technique and allows elementary and isotopic investigation of SOM on the surface of mineral particles, with a resolution of less than 100 nm (Herrmann et al., 2007; Heister et al., 2012). Due to its high spatial resolution and sensitivity, allowing the visualization and distribution of elements and isotopes, NanoSIMS is a powerful tool for studying organo-mineral interactions on the nanoscale. Remusat et al. (2012) confirmed that microorganism-derived OM binds preferentially to the surface of minerals through incubation assays using an isotopically labeled organic substrate, and NanoSIMS analyses combined with molecular information derived from X-ray transmission microscopy (STXM) measurements. Kopittke et al. (2020) obtained important information on the fate of OM recently added to the soil and the potential mechanisms by which it forms organo-mineral associations. Rumpel et al. (2015) reported that different processes produce organo-mineral associations according to soil depth; in the upper layers, the decomposed plant material can interact directly with metallic oxides, while in the deeper layers, the OM may interact with the metal oxides after microbial turnover. Finally, Kögel-Knabner et al. (2010) evidenced the transport of labeled amino acids inside soil aggregates through the pore network, demonstrating the potential of NanoSIMS to assess nanoscale biogeochemical processes that may contribute to C protection. Although NanoSIMS is a destructive technique, this method can preserve the spatial information of intact samples (Herrmann et al., 2007), allowing the study of organo-mineral associations while preserving the natural structure of soils.

Near-edge X-ray absorption fine structure (NEXAFS) spectroscopy is a high-resolution nondestructive spectroscopic tool for obtaining nanoscale chemical, structural, and orientational information about the sample of interest (Hemraj-Benny et al., 2006). This technique has been used to produce detailed information on the structural arrangement of organic matter as it can characterize specific C forms, including C-aromatic, C-aliphatic, and C-carboxyl (Schäfer et al., 2003; Lehmann et al., 2005; Kinyangi et al., 2006), as well as specific elements, minerals, metallic ions, and other architectural features of organo-mineral sets (Lehmann et al., 2007; Solomon et al., 2012). This provides a better understanding of biogeochemical processes and interactions relevant to SOM stabilization (Lehmann and Solomon, 2010). The NEXAFS can also be used to investigate the effect of land-use and management on SOM composition and dynamics at a molecular level (Lehmann et al., 2005). The NEXAFS combined with Fourier transform infrared spectroscopy (FTIR) allows mapping the content, location, and shape of C in relation to the mineral surface within aggregates. Although FTIR can produce high-resolution data when used alone, it can only obtain detailed information on the chemical composition of the SOM, but little information on the microenvironment.

Coupling NEXAFS with STXM, Lehmann et al. (2008) demonstrated that even at small spatial scales (less than 50 nm), C forms in intact microaggregates vary and can be identified (i.e., plants or microbial-derived biopolymers). The STXM-NEXAFS technique could elucidate the relationship between soil mineral elements (e.g., Ca, Fe, Al, and Si) and the different chemical C forms, such as the associations formed between metallic oxides and OM, which are important to SOM stabilization and persistence in tropical

environments (Solomon et al., 2012; Stuckey et al., 2017; Sowers et al., 2018). Combining STXM-NEXAFS techniques to elucidate organo-mineral associations at a submicron scale, Arachchige et al. (2018) found simple forms of C preserved within soil microaggregates, demonstrating that SOM stabilization is not governed solely by the chemical composition of the substrate. By mapping the distribution of different C forms in soil microaggregates, studies obtained detailed information on the importance of spatial inaccessibility for SOM stabilization. The STXM-NEXAFS was also used to explore if there are gradients of C concentration from the surface of aggregates to their interior, which in turn configures the occlusion of organic debris within the aggregate (Hernandez-Soriano et al., 2018).

### ***Non-destructive visualization analytical methods***

Major recent advances in the *in-situ* evaluation of SOM have been made through the use of non-destructive visualization methods, such as X-ray Computed Tomography (CT), which can provide a three-dimensional representation of the soil architecture and its constituents (Cnudde and Boone, 2013). Pores (occupied by air or water), organic matter, and mineral particles, present different densities and atomic compositions, causing different X-ray attenuations, measured by the amount of energy that is transmitted after the interaction with matter (Taina et al., 2008). When the X-ray passes through soil minerals, a lower intensity is produced in the detector due to strong attenuation, and the opposite occurs when it passes through an air-filled pore. Therefore, an image with different gray scales is obtained, providing information on the internal structure of the analyzed sample. The construction of microscale “maps” of soil aggregates showing the colocalization of minerals, roots, and microorganisms can increase the knowledge about the fate of soil OM, indicating potential microsites for its stabilization (Kinyangi et al., 2006). The diversity of microenvironments formed by the soil structure strongly influences microbial communities and the distribution pattern of these organisms in the soil (Young and Crawford, 2004), in addition to controlling the degree of interaction between organisms and SOM (Nunan et al., 2006; Kravchenko et al., 2019). As the physical microenvironment can be characterized, X-ray CT can reveal the porous architecture and location of organic matter within the aggregates (Baveye et al., 2010), allowing visualization of larger organic fragments (i.e., POM) and plant roots (Kravchenko et al., 2015).

Because CT does not allow researchers to view microorganisms in the soil, attempts to integrate X-ray CT into soil biological experiments have already been made (see Feeney et al., 2006; Bouckaert et al., 2013; Kravchenko et al., 2019; Lammel et al., 2019). Using X-ray microtomography combined with other techniques, Kravchenko et al. (2019) reported that pores with radii of 30–150 µm contain more active microorganisms that respond more quickly to C input. Therefore, in this pore size range, higher amounts of microbially-processed C are preferentially stabilized by various physicochemical mechanisms. Several other studies using CT have provided information about pore geometry, biogeochemical processes, and SOM protection (Peth et al., 2008), supporting the hypothesis that more continuous and interconnected pores favor the flow of C into the aggregates, which contribute to its stabilization and storage. However, the visualization of nonparticulate SOM remains a research challenge and, in part, the next step to the mechanistic understanding of SOM protection. As CT can characterize intact soil samples with a greater level of detail (Elliot and Heck, 2007), the combination of X-ray CT with other advanced techniques, such as spectroscopy, is a research priority to improve scientists’ ability to determine the biological, mineral, organic, and inorganic constituents within the soil structure (Dal Ferro et al., 2012; Rennert et al., 2012).

### ***Synchrotron radiation: a brilliant opportunity***

Use of synchrotron radiation for science applications began in the 1990s, in numerous disciplines. In soil and the environmental sciences, interest in the use of synchrotron radiation techniques has been growing since the pioneering studies by Hayes et al. (1987) and Brown and Parks (1989), who applied X-ray absorption spectroscopy (XAS)

to examine the mechanisms of ion sorption in geomaterials. The last two decades have seen great progress in the installation of synchrotron radiation sources, optical detectors, new spectroscopy techniques, and imaging techniques that can create molecular-level information (Luo and Zhang, 2010). Also associated with the scientific advances provided by synchrotron radiation techniques are the high density and coherence of flows, low divergence, and novel sample preparation techniques (Sharma and Hesterberg, 2020).

Literature contains excellent reviews on synchrotron radiation techniques based on their respective fields, detailing their different applications and limitations (Suortti and Thominson, 2003; Singh and Gafe, 2010; Sharma and Hesterberg, 2020). In SOM studies, of near-edge structure X-ray absorption spectroscopy (XANES) (e.g., Wang et al., 2019), extended X-ray absorption fine structure spectroscopy (EXAFS) (e.g., Giannetta et al., 2020), transmission X-ray microscopy (STXM) (e.g., Schumacher et al., 2005; Solomon et al., 2012), and X-ray microtomography ( $\mu$ CT) (e.g., Kravchenko and Guber, 2017) has been increasingly used. The EXAFS is one of the nondestructive techniques that can be used to determine the chemical species of C associated with different soil fractions whose sensitivity allows for detailing the linkage mechanisms between SOM and the mineral surfaces (Henneberry et al., 2012; Chen et al., 2014; Giannetta et al., 2020).

Similarly, X-ray microfluorescence ( $\mu$ -XRF) can map the distribution elements of interest within the soil matrix and their association with mineral particles, although it has only been minimally used in studies about SOM (Luster et al., 2009; Stuckman et al., 2019). Inagaki et al. (2020), using XANES, observed that in environments with high rainfall, there is an increase in more reduced Fe compounds, reducing the stabilization of SOM associated with this element, while for the same scenario, the associations between MO and Al dominate the stabilization of SOM, detailing the importance of this element in reducing conditions common in tropical regions. In contrast, synchrotron radiation-based Fourier transform infrared spectroscopy (SR-FTIR) can be used to evaluate the characteristics of the bonds between Fe and SOM, allowing the understanding of the role that surface sorption of SOM with Fe oxides plays in different soils and which compounds are preferentially stabilized by these oxyhydroxides (Wan et al., 2019).

The combination of high-resolution spectroscopy and imaging techniques based on synchrotron radiation can also be used to better study and visualize the processes that occur in the rhizosphere, such as improving the knowledge of the interactions between the SOM, mineralogy, soil structure, and roots (Raab and Lipson, 2010; York et al., 2016). Finally, to improve the knowledge of SOM dynamics and provide better parameters to develop mechanistic models of the potential of soils to store C, a more precise description of microorganisms and the organic substrate within the soil matrix is required (Monga et al., 2008; Ngom et al., 2011). Recently, great advances have been made in obtaining the three-dimensional localization of SOM in submillimeter aggregates through the combination of ( $\mu$ CT) and osmium tetroxide ( $\text{OsO}_4$ ) staining to observe small organic particles within the soil aggregates, which cannot be observed with traditional techniques (Peth et al., 2014; Arai et al., 2019; Zheng et al., 2020).

In general, synchrotron radiation techniques aim to obtain a mechanistic understanding of the biogeochemical processes and the factors that condition the stabilization of the SOM on a micro-scale. Synchrotron radiation techniques enable a new generation of scientific discoveries based on the investigation of SOM interaction mechanisms that occur on the micro- to the nanoscale scales and control large-scale processes (Sharma and Hesterberg, 2020). These new scientific opportunities are pivotal for the mechanistic understanding of SOM stabilization, particularly for obtaining advances in soils from tropical regions, where these mechanisms are still poorly understood.

### Research Opportunities on OM in Tropical Soils

Although the mineralogy of highly weathered soils has been extensively studied (Uehara and Gillman, 1985; Schaefer et al., 2008), knowledge of the combination of low-activity clays (i.e., kaolinite) and Fe and Al oxides affect the formation of organo-mineral associations is

still poorly understood (Impact of phyllosilicate mineralogy on organic carbon stabilization in soils, 2014). The magnitude by which climatic conditions can induce changes in organo-mineral associations is also an open field for scientific investigation (Kleber et al., 2015). Iron and Al oxides are often mentioned together as stabilizing agents; however, the role and relative importance of each in SOM storage varies depending on the environment (i.e., soil type, climate, and management).

Another scientific question that has not yet been investigated is the role of calcium (Ca) in the stabilization of SOM. It is widely recognized that the amount of exchangeable Ca correlates positively with the SOM content and stability. Barreto et al. (2021) evaluated the effect of Ca on the thermal stability of organo-mineral associations in a synthetic mixture of kaolinite, goethite, and aluminum oxides, simulating the mineralogy of the clay fraction of highly weathered soils, and observed that greater availability of Ca in the system can increase both the extent to which C is retained on the surface of minerals and its stability. However, the exact mechanisms that guarantee this relationship remain unknown.

Highly physically stable microaggregates (<1 mm in diameter) of Oxisols may have a high potential to protect SOM. However, more studies are needed to understand the physical protection mechanisms provided by the microgranular structure characteristic of Oxisols. Future investigations can determine the extent to which the spatial arrangement and internal architecture (i.e., connectivity and pore tortuosity) of microaggregates may cause the spatial inaccessibility of OM to microorganisms and create physical barriers that reduce the availability of oxygen and water to decomposers.

In the tropics, the growing adoption of integrated production systems (e.g., crop-livestock integration or crop-livestock-forest integration) aims to intensify the production of food, fiber, and fuel and reduce agricultural greenhouse gas emissions to mitigate climate change. In such agrosystems, several management strategies are used to stimulate soil biological activity, improve fertility, and favor the accumulation of SOM. However, the mechanistic understanding of how different management components can be used to maximize SOM persistence in integrated agricultural systems is still limited. Additionally, cover crops are increasingly being introduced in intensive tropical agroecosystems to increase SOM and benefit soils and crops. New research challenges arise from their use, as different botanical families or plant species have distinct ecological functions and biochemical compositions. Furthermore, the use of cover crop mixes adds yet another layer of complexity to the questions that remain open for investigation, as the mechanisms of plant biodiversification on modulating belowground biodiversity and, consequently, on SOM decomposition and C stabilization are still largely unexplored.

Filling these gaps is critical to improving the current understanding of SOM dynamics and the complex biogeochemical processes that occur on a small scale, which condition SOM accumulation in soils from the tropics. Finally, understanding how soil management practices can stimulate biological processes and C sequestration is essential to design management systems that efficiently favor long-term C accrual to maintain soil health and mitigate climate change.

## ACKNOWLEDGMENTS

We gratefully acknowledge the support of the RCGI – Research Centre for Greenhouse Gas Innovation (2020/15230-5), Bayer S/A (project – “Balanço de carbono em sistemas agrícolas: revelando o impacto da adoção de práticas de manejo sustentáveis nos estoques de carbono do solo e nas emissões de gases de efeito estufa”) and CNPq (311787/2021-5). In addition, we thank the support of the Center for Carbon Research in Tropical Agriculture (CCARBON) – FAPESP process 21/10573-4.

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